Chapter 25

DIK HEG

Monogamy pays

Experimental liaisons and threesomes

The oystercatcher shares with the bonobo (an ape closely related to the chimp) the distinction of being one of the few species known to use copulation to formalise the bonds between individuals – and perhaps to signal that bond to others as well. Monogamy pays, as long-term studies at Schiermonnikoog have shown. Oystercatchers that engage in threesomes have only limited breeding success.

Sometimes I wonder if I shouldn't have delved so deeply into nature. After a couple of years of studying biology your outlook on nature has changed completely. Once the chimpanzee appeared to be '*un savage noblesse*' but now you know him as a 'baby killer' that makes a meal of a monkey from time to time.

For me and doubtless many others the biggest change in our views on nature comes about during lectures on animal behaviour and evolution. Why does our view of nature and the human species change so abruptly?

For me the answer is simple: events that I had observed but could not explain were suddenly understandable because they became part of an overall pattern. As Darwin realised and described in 'On the Origin of Species' individuals compete with each other in order to ensure that as many of their own offspring as possible join the next generation.

The chimpanzee follows this mandate too. If the dominant male is deposed the new troop leader will attempt to kill all of the other males' offspring. The mother chimps will then become reproductively receptive again and the new leader can start a replacement wave of his own offspring. Infanticide is thus understandable from the standpoint of the individual prospects of the chief adult players, even though this involves periodic gruesome murders. The concept of natural selection emphasises that the chimpanzee as an individual is not concerned with the survival of the species in general, but only with the survival of his own genes. Members of your own species can thus be your worst enemies.

Does this new view of nature always paint a bleak picture of the world? Certainly not: Darwinian theory does not exclude co-operation between individuals. We'll take a look at the 'sunny side' of nature in this chapter.

Conspicuous males

Why are the males so often the showy sex? Everyone knows bird species where the male has an elaborate and beautifully ornamented tail (the peacock) or very elongate and curled tail (the birds of paradise), while among the mammals the enormous antlers of male moose and elk set them apart.

Figure 25-1.
A colour-ringed oystercatcher. We use rings marked with horizontal stripes, rather than letters or numbers. The width and relative position of stripes on the ring in combination with the colour create an individual code that is easy to distinguish in the field.

Figure 25-2.
Copulating oystercatchers.
(Photo: Jan van de Kam)

This phenomenon caught Darwin's attention, and he even wrote an entire book on the subject ('The Descent of Man and Selection in Relation to Sex'). At first he worried that their very conspicuousness would make showy males more vulnerable to predation than their more drab companions. But in a flash of insight Darwin provided a brilliant evolutionary argument: these showy males would overcome their disadvantage with regard to predators by obtaining a selective advantage in mating by more readily attracting females! He dubbed this process 'sexual selection', and his ideas have been amply justified by studies on insects, fish, mammals and birds. Females really are attracted by showy males: these are preferred either because they provide better genes, or because they are better fathers when it comes to providing parental care.

There are some species where the roles are reversed, for example, female phalaropes and dotterels have more conspicuous and colourful plumage than males. In these species the drab males chose the mates, then care for the eggs and young without any help from the female (who flits off in search of other males). Sometimes the female ends up caring for one final clutch on her own.

Males can have several mates (*polygyny*, the lek system) as can females (*polyandry* = several males at once, *serial monogamy* = a succession of males as occurs in 'double clutching'). There are some species with even more complex mating systems. By marking individuals with unique colour-coded rings (Fig. 25-1) an observer can sort out these intricacies, and many discoveries await the patient and meticulous researcher.

Being choosy

On the hundredth anniversary of Darwin's original book every aspect of his ideas was reviewed. On this occasion Robert Trivers emphasised that we can only understand the evolutionary origin of the various mating systems if we consider sexual selection and the evolution of parental care side by side. Because females always face a limit in the number of eggs they can lay, it will always pay to be discriminating in selecting a male partner rather than grabbing the first to come along. Females are thus considered the 'choosy sex'.

Males on the other hand can produce enough sperm to mate successfully with many females. Males should attempt to mate with many partners, and they need not be so choosy. This principle of extra matings whenever the opportunity arises also applies in species that are socially monogamous: even though one male and one female inhabit a

territory together, the male will attempt copulation outside the pair bond (for example, with neighbouring females, Fig. 25-2).

Nowadays we can trace parentage in behavioural studies on natural populations using sophisticated molecular techniques (for example, DNA-fingerprinting, a genetic method that has acquired a degree of notoriety from its use in criminal cases). All you need is a tiny drop of blood from the cast of characters, and you can find out if the *extra-pair* copulations actually result in *extra-pair* young (see Fig. 25-3). In some bird species this technique has revealed that extra-pair young can comprise more than half of the young hatched! Top males can thus sire far more young than would be possible with only one partner. The point to remember is that there is a tremendous skew in the proficiency of males at obtaining extra-pair young.

Females are prepared to mate with 'good' males provided that this enhances the survival and future reproductive success of their progeny. Even if you cannot keep this 'good' male all to yourself in an exclusive monogamous bond, it is still advantageous to make use of his genes by accepting an extra-pair mating with such a 'high quality' male.

Co-operation under duress

In some long-lived bird species, such as geese and oystercatchers, the male and female live in social monogamy characterised by very low rates of extra-pair young. How can we explain this? Perhaps in some subtle way their faithfulness is a secret weapon enforcing co-operation in parental care. Research has suggested that a male is more likely to help feed and care for the nestlings if he is certain of his paternity.

In many bird species the female is capable of raising her young alone, but this is not true of oystercatchers (or geese). If we capture and remove one oystercatcher on the nest the remaining parent is unable to raise the young alone. In every case the solo partner loses the nest, and in about half of all cases the entire territory is lost as well! Apparently

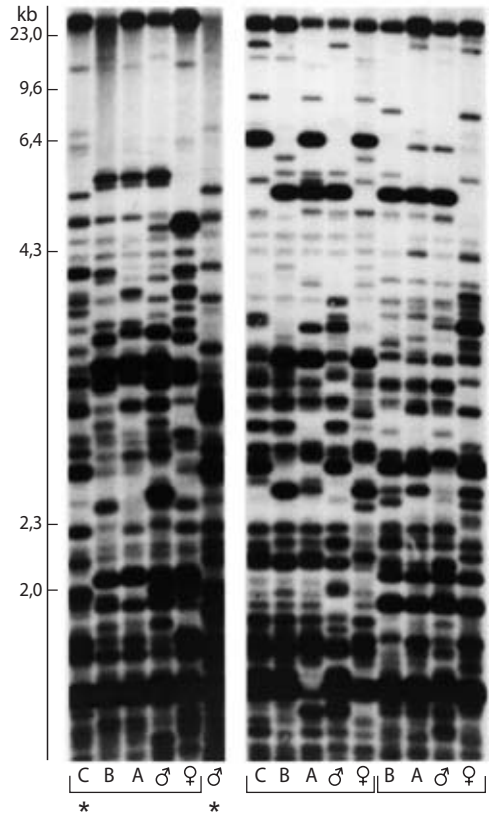

Figure 25-3.
DNA fingerprints of oystercatcher chicks and their parents from three families in 1989. Each band represents a specific DNA fragment, and the individuals are shown as vertical stacks (identity along bottom, chicks are A, B, C). Each chick should receive about as many bands from the mother as from the (genetic) father. In this example all young are the offspring of the putative parents, with one exception marked with an asterisk*. The genetic father of this chick turned out to be the neighbouring male (also marked with*). The mother was observed to copulate frequently with this neighbour before laying, and eventually chased away the original partner and became the mate of the *male.

the advantage of sharing parental care is so great in this species that the female oystercatcher does not dare to put this at risk by indulging in copulations with extra-pair males. Within the mated pair copulations are frequent, and perhaps this is one way the female makes sure that the male will continue with territorial defence and parental care.

From our observations on Schiermonnikoog we found that mated pairs copulated on average once every hour when out on the mudflats, and extra-pair copulations were

rather rare (only 3 percent of all copulations involving marked participants). The evolution of mating systems and patterns of parental care are thus intertwined. These two behavioural repertoires are so tightly locked together that it does not pay the oystercatcher male to maintain close bonds with more than one female. Or that is my interpretation of our 20 years of work on the Schiermonnikoog population.

Is two plus one less than three?

22 May 1992. Nest check area B nearby Beacon 25

A seventh egg has been laid in nest 20! There are now four eggs from the first wife (Anna) and three from the second (Bea), all in the same nest cup. Bea was obviously on the point of laying when we saw her yesterday on the mudflats with her protruding abdomen, and has since laid her last egg. The male Menno is a polygamist. He has been in a polygynous relationship since 1984, first with Bea and Clara, but after the severe winter of 1986-1987 Clara departed for happier hunting grounds and Anna has taken her place. Two females, seven eggs; this promises to be interesting!

Since the 1950s very large oystercatcher clutches have been found, both in England and in the Netherlands (Fig. 25-4). Judging from the eggs' background colour and patterning these super clutches are the products of two females that have laid in the same nest. So it's a case of polygyny, but the shared egg care makes it a special case. Group nesting is known from the New World (the acorn woodpecker and the groove-billed ani) but amongst oystercatchers it is an exceedingly rare phenomenon. Only 1 percent of territories are home to a co-operative polygynous trio (Fig. 25-5).

27 May 1992. Nest check

Something is wrong with nest 20: eggs 2, 4, 5 and 7 are warm and clustered in the nest cup, but eggs 1, 3 and 6 are partly outside and feel cold. What will happen if all of the eggs are not incubated properly? So far we have only seen one bird on the nest at a time: either the male or one of his two wives. Normally it is easy for an oystercatcher to keep four eggs (the maximum monogamous clutch) warm, but seven is clearly more than they can manage.

3 June 1992

There are three cold eggs in nest 20 again, but this time they're numbers 4, 5 and 7.

27 June 1992

Nest 20 has been abandoned: after 35 days the parents have apparently lost all hope of hatching an egg. All seven eggs are stone-cold in the nest cup, and the parents no longer make alarm calls when we approach. The trio, incubating one at a time, has never been able to keep more than four eggs warm, and with the constant rearranging no single egg received enough warmth to hatch.

I conducted some experiments to test if a clutch of four really represents the maximum a parent oystercatcher can incubate effectively, given the dimensions of the brood patch (a bare and highly vascularised area of belly skin that transfers warmth from the parent to the eggs) and the way the eggs fit together. Oystercatcher parents were presented with four, five or even six copper eggs, of the right size and painted to resemble real eggs. Inside the egg a thermal sensor was mounted on a memory chip that continuously recorded egg temperature over a 48-hour period. An example of the results is displayed in Fig. 25-6.

Oystercatchers are indeed unable to keep more than four eggs warm at any one time. Luckily in some trios, the participants lay fewer eggs so that the total in the nest is only three or four, with better results than nest 20. Nevertheless hatching success is only 49 percent on average in co-operatively incubating polygynous nests, compared to 83 percent in conventional monogamous nests. Aside from losing eggs to predators such as gulls, trios have poor prospects due to their inability to provide the eggs with sufficient warmth.

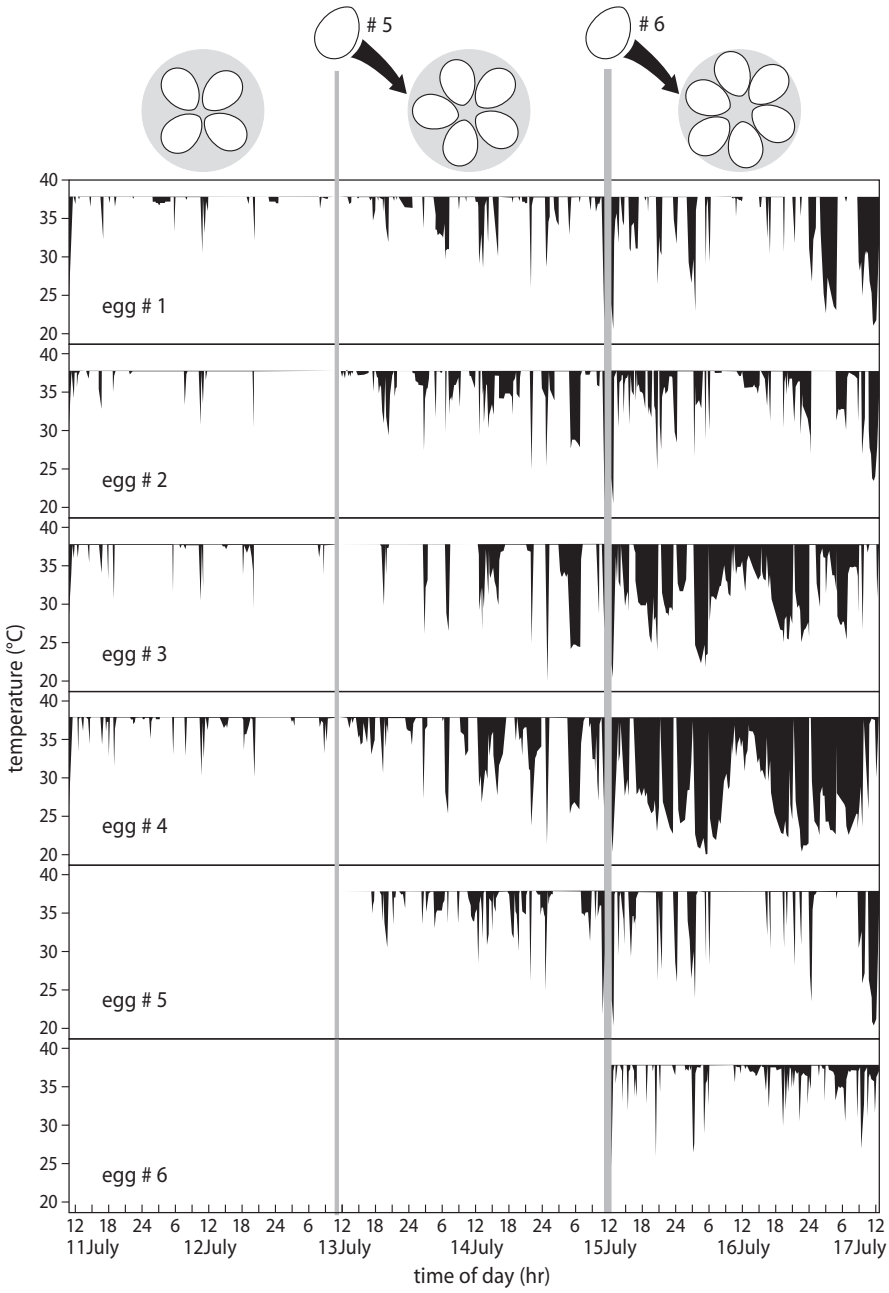

Figure 25-6.
Oystercatchers are unable to keep clutches of more than four eggs warm. Temperature recordings from hollow copper eggs (#1-4) that temporarily replaced the real eggs are shown. Each copper egg contains a miniature thermal sensor recording temperature every minute on an inbuilt chip. After two days (time scale along bottom) the clutch of four was increased by adding copper egg #5, and after another two days copper egg #6 was inserted. With a clutch of five or six eggs the parents are unable to keep all eggs warm (shortfall highlighted in black).

9 March 1993. Trio near Beacon 25

The male Menno has not yet turned up after the winter. The two females (Anna and Bea) jointly defend the territory against the neighbours. At 13.08 Bea suddenly initiates an approach towards Anna as though she were the male about to initiate copulation: sleeked feathers, stiff and jerky movements, rapid

Figure 25-4.
The clutch of a trio (top) compared to the normal four egg clutch of a monogamous pair (below).

pacing accompanied by calling. Anna evades, but the next minute Bea tries again, and this time copulation is achieved and is to all appearances perfectly normal (neither sex possesses a penis and during copulation the cloacal openings are simply pressed tightly together; although the male is usually on top this is not always the case).

Somewhat dazed I continue on my rounds and try to fit this sighting into my frame of reference. Although I had observed copulations between birds of like sex before, especially among nonbreeding oystercatchers, I had always considered these to be cases of mistaken identity. Perhaps it was difficult for the participants to determine gender, because male and female oystercatchers look very similar. This reasoning could not apply to the Anna-Bea episode, as they had nested communally for years and had defended the territory together with the male Menno; they must know each other intimately!

Closing the case

12 March 1993
An unringed male (caught later in the season, ringed and named 'Nico') has taken the place of old Menno who failed to return after the winter. The two females copulate with one another, and Anna copulates with the new male as well.

In the harsh winter of 1995-1996 a neighbouring female dies and the threesome split up for good. Anna moves over and becomes the partner of the neighbouring widower. Both Anna with her new mate, and Bea with Nico, in their new monogamous relationships fledge young, so obviously both females were fertile all along.

How do co-operative trios arise?

Watching nest 20 and other co-operative trios I began to appreciate why they produced so few young compared to monogamous pairs (as depicted in Fig. 25-7). But I still did not know how these trios originated. Collecting enough case histories to build a scenario was a long-term job, because polygamy is so rare among oystercatchers.

In all I collected data on this topic over eight seasons on Schiermonnikoog (1990-1997) and increased the study area to cover more nests. Trios accounted for only 1 percent of the territories. The vital clue to understanding how these trios arise came from considering the 'aggressive polygynous trios' another infrequent variant (1 percent of all territories) but well known from other bird species like the blue tit. Such trios arise when a female breaks in on a monogamous pair on the breeding territory and tries to chase away the incumbent female.

7 March 1993. Area A
The situation along the creek looks pretty

Figure 25-5.
A trio on their breeding territory on the salt marsh.
(Photo: Jan van de Kam)

grim. During the 1987-1992 breeding seasons the neighbouring pairs of Otto/Clara and Pietro/Dana lived in peace, with only ritual territorial border disputes on their boundary. But with the death of Otto in the winter of 1992-1993 an explosive situation arose. Clara is now alone and on the market for a new mate – and she has her eye on Pietro, even though they were officially enemies for all those years. Despite previous disputes, Clara knows that Pietro was a caring parent in the past, and starts her campaign against Dana. Vehement disputes in the form of 'piping ceremonies' and 'butterfly flights' over the neighbouring territory conveying the message 'this is now mine' follow, as do charges aimed at each other's vulnerable heads! At first Pietro tries to help his mate Dana keep Clara out, but soon gives up. The fights intensify, an eye for an eye, a tooth for a tooth.

Fights like this usually end in the classic winner/loser outcome. As well as 'widows' like Clara, nonbreeding females may also try to fight their way into breeding status with a mate by deposing his territorial female. But sometimes there is no clear outcome: neither of the contestants is willing to give up. In the case of neighbouring females each may make

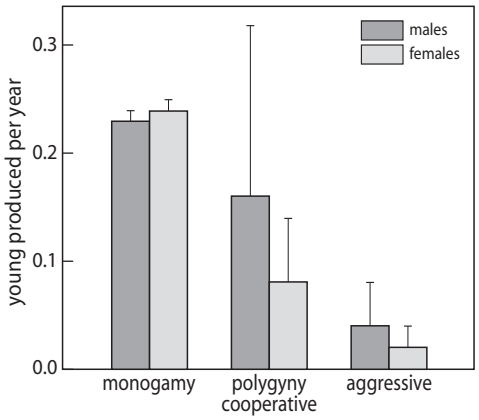

Figure 25-7.
Sharing a male with another female reduces breeding success; more is not always better. The number of young fledged *per parent* for monogamous pairs is shown compared to that of co-operatively breeding trios (centre) and aggressive trios (right). For polygynous males the production of both of their mates has been summed.

a nest in their territory, and share the male! Such aggressive polygynous trios have the lowest success of all (Fig. 25-7) because many eggs are lost during the continuous territorial strife, and the remainder have poor prospects since the male cannot protect both nests effectively against predators.

For the entire 1993 season Clara and Dana continue hostilities, and in the winter 1993-1994 they are even observed fighting on the feeding territory on the mudflat! We expect a solution to emerge in spring 1994: in our experience such aggressive trios do not last long. But who will be the winner?

15 April 1994. Mudflat bordering area A, time 16.16

Dana approaches Clara in what I am sure will end in another fight, but to my amazement Dana suddenly takes on the pose typical for a female soliciting copulation with cocked tail. Clara reacts cautiously to this radical reversal of their relations and although she approaches with male-like posturing does not carry on by jumping atop her erstwhile rival. Up until the end of May aggressive incidents are still observed between the two, but these incidents are now regularly interspersed by female-female copulations (sometimes Clara on top, sometimes Dana). Thus they established a *co-operative polygynous trio* with the male Pietro for the 1994 season.

In 1995 we observed the initiation of several other co-operative trios, and in all cases the females copulated with one another as had Dana and Clara. The puzzle of how such co-operative trios arise is thus explained by the transition from an originally aggressive threesome, as soon as the contesting females bury the hatchet. But where are the advantages of this curious arrangement?

The famous kinship rule formulated by Hamilton (in 1946) states that you might expect such co-operation if the females are related to one another. Rob van Treuren followed this up for our oystercatchers by analysing the DNA from 118 females sampled in the field. Unfortunately for the theory, females in the trios were not more closely related to one another than any other two breeding females drawn from the population.

Nevertheless, if neither of the disputing females is clearly a winner, the best option in the short-term might well be to get together in the hope of producing at least some young that season. Although the output is less than that of a monogamously mated female, it is still much better than nothing at all, the alternative facing a rejected nonbreeder. Moreover the polygynous female has a much better chance of becoming a monogamous female the next season (60 percent of cases) compared to starting again from the nonbreeder status (only 10 percent obtain a mate and territory). By joining a rather weird polygynous trio, the female gains a stepping stone towards the higher reproductive reward of monogamy. Aside from the bonobo (a close relative of the chimpanzee) the oystercatcher is the only species where co-operation is finalised (and perhaps signalled to others) by copulating.

More females aren't always better

What does the oystercatcher male hope to gain from multiple mates? Not much it seems; their reproductive success is less than that of males that have only one female (Fig. 25-7). But if they do not stand to gain by having a second female, why don't the males chase away the supernumerary?

We must remember that this is what generally happens: the male usually chases females away, and is willing to fight them (even though they are slightly larger). But you never know: perhaps the invading female might be a better mate than the old one. It might be the best policy for the male to let the females fight among themselves, and take whoever wins. If neither wins, this *laissez-faire* policy results in the male having two females and thus a lowered reproductive output that season. The costs of repeatedly chasing away a persistent invader (who promptly lands again after a token retreat) are apparently too high.

Amongst oystercatchers, the young's need

for care from both parents results in a basically monogamous breeding season, just as Trivers predicted 30 years ago. But the reward of our many years of oystercatcher watching is that we have been able to evaluate the competing parental styles. Individuals following the minority variant of polygyny give insights into how co-operative behaviour might evolve. The 'co-operative trios' in our observations represent a primitive form of group living. Evolution is always on the job, and whether future generations of oystercatchers will finally be able to break free from the monogamous mating pattern will be a challenge for future generations of behavioural ecologists!

References
44, 45, 78, 79, 80, 106, 107, 108, 109, 110, 111